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Hydraulic habitat use with respect to body size of aquatic insect larvae: Case of six species from a French Mediterranean type stream

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Abstract

Macroinvertebrates play a key role in lotic ecosystems, as fish prey and processors of organic material. Therefore, their hydraulic preferences have to be integrated in instream habitat models for ecological stream management. This study characterized physical habitat use in terms of shear velocity for the larvae of three Ephemeropteran (*Ephoron virgo*, *Oligoneuriella rhenana*, and *Serratella ignita*), two Trichopteran (*Cheumatopsyche lepida* and *Hydropsyche exocellata*) and one Dipteran species (*Blepharicera fasciata*) in a Mediterranean stream at a relatively low water discharge. *O. rhenana, C. lepida, H. exocellata*, and *B. fasciata* larvae were mainly found in high shear velocity conditions, whereas *E. virgo* and *S. ignita* larvae were found in low shear velocity conditions. Knowing that habitat preferences should vary during ontogenesis (with respect to changes in biological requirements and/or morphological abilities to withstand high flow, for example), our second objective was to characterize differences in the hydraulic habitat use (in terms of shear velocity) for different size classes of these six species.

Larvae of *H. exocellata* and *B. fasciata* mainly colonized high shear velocity conditions and numerous individuals of these species also used medium shear velocity conditions, independent of size class.

The use of high shear velocity conditions increased with larval size for *C. lepida* and *O. rhenana*, whilst the use of low shear velocity conditions increased for larger larvae of *E. virgo* and *S. ignita*. Various hypotheses are proposed to explain these different strategies of habitat use during ontogenesis. We point out the lack of knowledge about physical habitat shifts during the larval growth of freshwater invertebrates.

These results highlight the interest to consider the respective habitat requirements of different size classes of invertebrates in instream habitat models. Population bottlenecks should be overcome if hydraulic conditions are kept suitable for all size classes by stream managers.

Keywords: Stream ecology; Physical habitat use; Benthic invertebrates; Shear velocity; Ecological and biological traits; Size classes; Larval growth; Instream habitat models; Flow management

Introduction

In rivers, near-bed hydraulic constraints determine the distribution of benthic invertebrates (Statzner, 1981; Statzner & Higler, 1986). They directly structure the

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physical habitat and indirectly affect biotic interactions through resource availability, competition, and predation processes (Hart & Finelli, 1999). Some species are known to live in areas of low hydraulic constraints (e.g. near the bank), whereas others colonize fast-flowing zones with higher constraints (Dolédec, Lamouroux, Fuchs, & Mérigoux, 2007; Mérigoux & Dolédec, 2004). These differences in habitat use can largely be explained by differences in the ecological traits of species, such as feeding behavior or oxygen demands (Collier, 1994), but also by biotic interactions (Hansen, Hart, & Merz, 1991).

Macroinvertebrates play a key role in lotic ecosystems functioning, due to their dual role as fish prey and processors of organic material. Being less mobile than fish, most macroinvertebrates lack the ability to return to a previously inhabited area (Gore, Layzer, & Mead, 2001). With a short life cycle, they respond rapidly to environmental changes and are therefore very good indicators of the integrity of the quality of aquatic systems. Predictions from the Instream Flow Incremental Methodology (Stalnaker, Lamb, Henriksen, Bovee, & Bartholow, 1995) have demonstrated that, following changes in river discharge, the loss of macroinvertebrate habitat could be two- or three fold greater than the loss of fish habitat. In this context, Gore et al. (2001) recently called for integrating hydraulic preferences of invertebrates into habitat models. Therefore, many recent studies have considered the habitat use of benthic invertebrates for near-bed hydraulic conditions and have developed preference curves for hydraulics parameters (e.g. Brunke, Hoffmann, & Pusch, 2001; Dolédec et al., 2007; Mérigoux & Dolédec, 2004; Scheder & Waringer, 2002).

It was clearly demonstrated for fish that numerous species show differences of hydraulic habitat use during development (Mann, 1996; Sagnes, Champagne, & Morel, 2000; Schiemer, 2000), and habitat preferences are usually established for different size classes (e.g. Lamouroux, Capra, Pouilly, & Souchon, 1999). This is of great interest for stream management, as these different preference curves could be used to determine suitable habitat conditions for each size class. Physical conditions inducing potential population bottlenecks could therefore be estimated (Capra, Breil, & Souchon, 1995). In contrast to fish, habitat preferences of the numerous benthic invertebrate species are either estimated at a higher taxonomic level (e.g. generic or family level for Diptera) or at the species level but mixing all size classes (Dolédec et al., 2007; Extence, Balbi, & Chadd, 1999). However, like fish, hydraulic habitat preferences of invertebrates are likely to change during growth. For instance, hydraulic habitat of first instar larvae may be partly linked to the hydraulic conditions where egg masses are deposited by females and may be different than older larval stage preferences (e.g. Reich & Downes, 2004). Moreover, some Ephemeropteran and Plecopteran species progressively shift from high to low velocity habitats in the riparian zone prior to emerging (Alba-Tercedor, 1990; Hynes, 1976; Studemann, Landolt, Sartori, Heti, & Tomka, 1992) and some Trichopteran species shift their diet while growing, implying changes in their microhabitat use (Basaguren, Riano, & Pozo, 2002).

Rather than larval stages, which are sometimes difficult to determine, body size could be a good metric to be related to habitat use for aquatic organisms. Statzner and Borchardt (1994) showed that simply due to the increase of body length during development, aquatic organisms have to deal successively with different physical habitats. The Reynolds number (used to identify laminar or turbulent flow regimes around a body) of these organisms is proportional to the product of body size and flow velocity (see Statzner, 1988). Therefore, Statzner and Borchardt (1994) suggested that some aquatic insect larvae may successively use lower and lower velocity habitats as they grow to maintain in approximately constant hydraulic conditions. Moreover, intraspecific comparisons of different fish populations showed that habitat shifts were related to morphological shifts (i.e. changes in body size and shape during growth), which did not coincide with shifts from one developmental stage to another (Hedtke, Gaudin, Sagnes, & Bohle, 2001).

Shifts in habitat use during growth should partly explain the variability of habitat use in space and time observed for many species when different size classes are not separately considered (see examples in Dolédec et al., 2007). Therefore, studies characterizing hydraulic preferences of a given species should consider different size classes to better understand its strategy of habitat use. In this way, a few studies have related invertebrate body size to hydraulic parameters such as flow velocity (Collier, Croker, Hickey, Quinn, & Smith, 1995; Osborne & Herricks, 1987; Poff & Ward, 1992), substratum particle size, or roughness (Buffagni, Crosa, & Marchetti, 1995; Gee, 1982; Pringle, 1982; Rees, 1972; Williams & Moore, 1986), or near-bed hydraulic constraints (Martin, 1985; Statzner & Borchardt, 1994).

In this context, the objectives of this study were (1) to describe the distribution of the aquatic larvae of six insect species [two Trichopteran species: *Cheumatopsyche lepida* (Pictet), *Hydropsyche exocellata* Dufour, three Ephemeropteran species: *Ephoron virgo* (Olivier), *Oligoneuriella rhenana* (Imhoff), and *Serratella ignita* (Poda), and one Dipteran species: *Blepharicera fasciata* (Westwood)] along a shear velocity gradient in a Mediterranean stream at a relatively low flow discharge and (2) to examine these relationships for different size classes of these species.

Methods

We sampled invertebrates in one reach of the lower Ardèche River which is a Mediterranean-type tributary of the Rhône River situated in southern France (Fig. 1). The drainage basin (2429 km^2) is characterized by tributaries with steep slopes on calcareous bedrock. Annual mean discharge is about 63.5 m^3/s at the sampled reach, which is 84 km downstream of the source within a deep canyon (see Mérigoux & Dolédec, 2004 for more details about this river).

We sampled in June 2000 ($n = 34$, discharge = 12 m^3/s), using a modified Surber sampler (area 0.1 m^2, mesh size 500 μm). Samples were taken from down- to upstream over a length of 800 m and across the width of the river. As the whole available habitat has to be sampled to establish relevant habitat use, we took sample units that covered the full near-bed hydraulic gradient of the reach (see below). For each of the sample units, we collected organisms by stirring and removing the surface sediments to a depth of a few centimeters. We brushed the largest stones to collect any attached invertebrates and preserved the sample units in 4% formaldehyde. In the laboratory, we identified invertebrates to the lowest possible taxonomic level, mainly using keys in Tachet, Richoux, Bournaud, and Usseglio-Polatera (2000).

After sampling invertebrates, we used "Fliesswasserstammtisch" (FST) hemispheres (Statzner & Müller, 1989) to measure near-bed hydraulic forces at the point at which the Surber had been used. This simple method involves the use of 24 standard hemispheres of identical size (diameter 7.8 cm) and surface texture, but different densities. Hemispheres are exposed sequentially on a small weighted horizontal Plexiglas plate on the stream bottom and the heaviest hemisphere just moved by the flow defines the instantaneous flow conditions near the stream bottom. Each hemisphere provides an estimate of the minimum bottom shear stress (MBSS) force in N/m^2 causing the movement of this given hemisphere. For instance, hemisphere number 0 and 17 indicate a MBSS of 7.71×10^{-2} and 6.34 N/m^2, respectively (see details of FST-hemispheres calibration in Statzner, Kohmann, & Hildrew, 1991). Shear velocity (U^*, in cm/s) at each sample can subsequently be calculated by the following: $U^* = (\text{MBSS} \times 10)^{0.5}$. The shear velocity gradient in our studied reach ranged from 0.88 to 7.96 cm/s at least (and up to a maximum of 9.46 cm/s, corresponding to the minimum shear velocity measured by hemisphere number 18, which never moved during the sampling). We usually took two sample units in each near-bed hydraulic condition (i.e. in each hemisphere number), except for shear velocities of 1.09 and 1.98 cm/s (only one sample). In these cases, the number of individuals in the unique sample was multiplied by two in the analyses. To simplify the presentation of results, we will refer hereafter to low, medium, and high shear velocities, arbitrarily defined as [0.88–1.48] cm/s (hemispheres number 0–5), [1.48–3.30] cm/s (hemispheres 6–11) and [3.30–9.46] cm/s (hemispheres 12–17), respectively. Note that particle size of the mineral substrata was comparable between samples (mainly cobbles and coarse gravel, with fine sediments within interstices).

The six species studied were selected because they were abundant over the entire shear velocity gradient we sampled. We collected size measurements for a minimum of 160 individuals for *B. fasciata* and up to a maximum of 1212 individuals for *H. exocellata*. We used a tri-ocular lens to take invertebrate digital pictures and the ImageJ 1.27z software (freeware, available at http://rsb.info.nih.gov/ij/) to measure individual body lengths. Compared with the traditional binocular lens and micrometer, this image analysis method minimizes measurement errors especially for small organisms (Sagnes, 1995). When bodies were not straight, we determined body lengths by drawing and measuring a lateral line following body curvatures. Body lengths

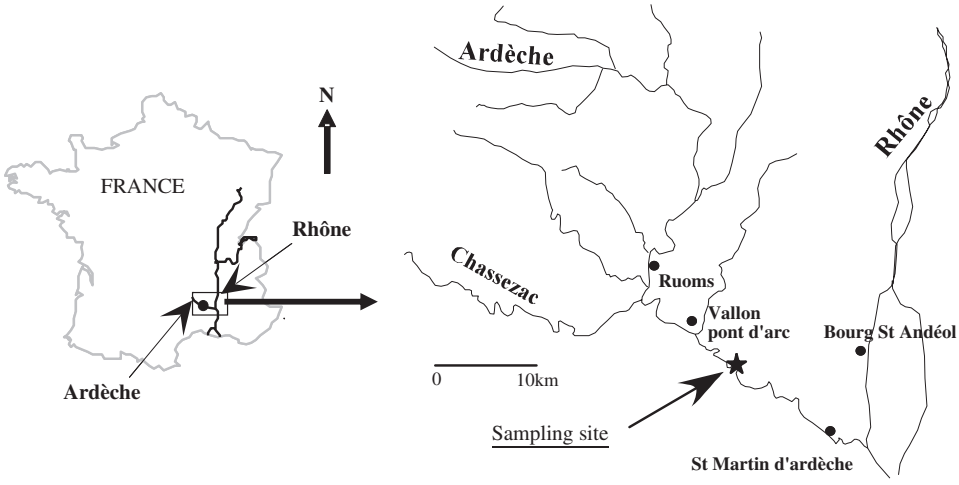

Fig. 1. Sampling location (Ardèche River, France).

corresponded to the distance between the most anterior part of the head (except antennae) to the abdominal distal extremity for Trichopteran and Ephemeropteran species. It was impossible to measure the total length of *B. fasciata* larvae. Their slightly sclerotized body is composed of one cephalic and six abdominal segments, each separated by an intersegmental membrane, and bears 6 ventral suckers (the last abdominal segment has no sucker). This body organization enables them to move by contraction of their segments like an accordion. When preserved in formaldehyde, individuals can be fixed in different contraction levels and total length measurements become impossible without strong bias. Therefore, for *B. fasciata*, we measured labrum width [we chose this measurement because it is completely sclerotized and thus less deformed during preservation than non-sclerotized body parts (Distefano, Roell, Wagner, & Decoske, 1994)] and we assumed that total length was proportional to labrum width.

There were three apparent size classes of labrum width for *B. fasciata* but no apparent cohorts in the length–frequency distributions of the five other species. Therefore, we arbitrarily determined three size classes for these species by calculating three identical intervals between the respective lengths of the smallest and the largest individuals (i.e. size class 1 = small, size class 2 = intermediate, and size class 3 = large individuals). When the number of individuals in a size class was less than 30 (which was the case for size class 1 of *O. rhenana* and *B. fasciata*, and size class 3 of *S. ignita*), these individuals were grouped with those of the next closest size class.

Habitat use is presented as percentage of individuals at a given shear velocity, for each species (i.e. using all the individuals sampled) and size class within each species. χ^2 tests with Yates corrections were used on the percentages to check for differences in habitat use between the different size classes.

Results

Shear velocity use of larvae

Within a species, individuals were not randomly distributed along the gradient of shear velocity. *O. rhenana, C. lepida, H. exocellata*, and *B. fasciata* larvae were mainly found in high shear velocity conditions (71%, 59%, 51%, and 56% of the total individuals, respectively, Table 1, Fig. 2). Many individuals were also found in medium shear velocity conditions for these four species (between 26% and

Table 1. Proportion (%) of larvae found in different shear velocity environments

Order	Species and size class	Size range (mm)	In L (%)	In M (%)	In H (%)	*n*
Ephemeroptera	*Ephoron virgo* (all)	1.92–10.16	75.00	18.43	6.57	700
	E. virgo 1	1.92–4.82	65.06	23.80	11.14	332
	E. virgo 2	4.82–7.71	82.88	14.41	2.70	333
	E. virgo 3	7.71–10.16	94.29	5.71	0.00	35
	Oligoneuriella rhenana (all)	1.93–18.07	3.51	25.96	70.53	285
	O. rhenana 1+2	1.93–12.69	4.49	32.02	63.48	178
	O. rhenana 3	12.69–18.07	1.87	15.89	82.24	107
	Serratella ignita (all)	1.29–9.84	67.92	21.89	10.19	265
	S. ignita 1	1.29–4.14	52.50	33.75	13.75	80
	S. ignita 2+3	4.14–9.84	74.59	16.76	8.65	185
Trichoptera	*Cheumatopsyche lepida* (all)	0.85–5.83	2.88	38.35	58.77	798
	C. lepida 1	0.85–2.51	3.10	48.34	48.56	451
	C. lepida 2	2.51–4.17	2.85	27.85	69.30	316
	C. lepida 3	4.17–5.83	0.00	0.00	100.00	31
	Hydropsyche exocellata (all)	1.16–16.61	13.86	35.48	50.66	1212
	H. exocellata 1	1.16–6.31	11.19	36.35	52.45	795
	H. exocellata 2	6.31–11.46	18.40	33.74	47.85	326
	H. exocellata 3	11.46–16.61	20.88	34.07	45.05	91
Diptera	*Blepharicera fasciata* (all)	0.25–0.73	1.25	43.13	55.63	160
	B. fasciata 1+2	0.25–0.47	3.28	39.34	57.38	61
	B. fasciata 3	0.55–0.73	0.00	45.45	54.55	99

[*L* = low (0.88–1.48 cm/s), M = medium (1.48–3.30 cm/s) and H = high (3.30–9.46 cm/s) shear velocities] for six species of aquatic insects. Size classes of each species were combined (all) or separated into three size classes numbered from 1 (small individuals) to 3 (large individuals). Note that size range of each size class corresponds to body lengths for all species but *B. fasciata*, for which size range corresponds to extrem labrum widths (see methods). When the number *n* of larvae in a size class was less than 30, they were grouped with those of the neighboring size class.

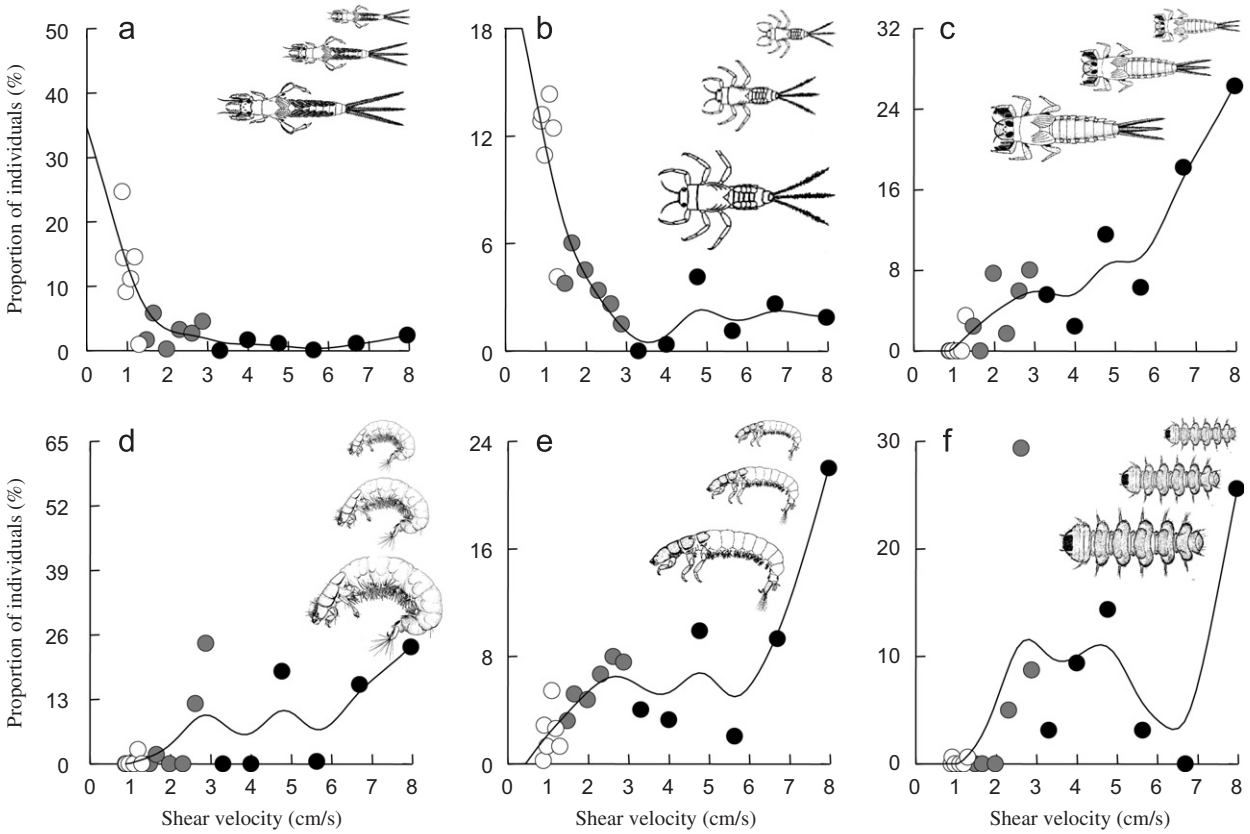

Fig. 2. Proportion of individuals (%) found in different shear velocity (cm/s) environments for all individuals of six insect species: (a) *E. virgo*, (b) *S. ignita*, (c) *O. rhenana*, (d) *C. lepida,* (e) *H. exocellata*, and (f) *B. fasciata*. For each species, size range and number of individuals used in the analyses are given in Table 1. Note that the scales of *y*-axes differ among species. White, gray, and black dots represent low (L), medium (M), and high (H) shear velocity classes, respectively (see text and Table 1). Indicative trends (curved lines) were estimated using a least squares smoothing. Insect drawings from Tachet et al. (2000).

43% of the total individuals for *O. rhenana* and *B. fasciata*, respectively). *E. virgo* and *S. ignita* larvae were mainly found in low shear velocity conditions (75% and 68% of the total individuals, respectively, Table 1 and Fig. 2). A significant percentage of individuals were also found in medium shear velocity conditions for these two species (18% and 22% for *E. virgo* and *S. ignita*, respectively).

Shear velocity use of larvae for different size classes

Whatever the size class considered, most individuals of *C. lepida*, *O. rhenana, B. fasciata* (>95% of the individuals for these three species), and *H. exocellata* (>79% of the individuals) were found in medium or high shear velocity conditions (Table 1, Figs. 3 and 4). For *H. exocellata* and *B. fasciata*, proportions of individuals in each hydraulic condition were comparable between the different size classes (not significant χ^2, Fig. 4). The only exception was size class 1 of *H. exocellata*, which occurred less frequently in low shear velocity conditions compared to other size classes (χ^2, $p<0.01$ between size classes 1 and 2, and $p<0.05$ between size classes 1 and 3). In contrast, proportion of individuals increased in high shear velocity conditions with increasing body sizes for *C. lepida* (χ^2, $p<10^{-6}$ between size classes 1 and 2 and $p<0.001$ between size classes 2 and 3; all the largest individuals were collected in high shear velocity conditions, Fig. 4) and *O. rhenana* (χ^2, $p<0.01$ between size classes 1–2 and 3, Fig. 3) while the proportion of individuals in medium shear velocity conditions decreased with body size for these two species (χ^2; $p<10^{-6}$ between size classes 1 and 2 and $p<0.01$ between size classes 2 and 3 for *C. lepida*; $p<0.01$ between size classes 1–2 and 3 for *O. rhenana*).

An opposite pattern was found for *E. virgo* and *S. ignita*, where individuals were mainly found in low shear velocity conditions, regardless of size class (>52% of all the individuals) (Table 1 and Fig. 3). For *E. virgo*, the proportion of individuals in low shear velocity conditions increased to a total of about 94% for the largest individuals. This change was statistically significant

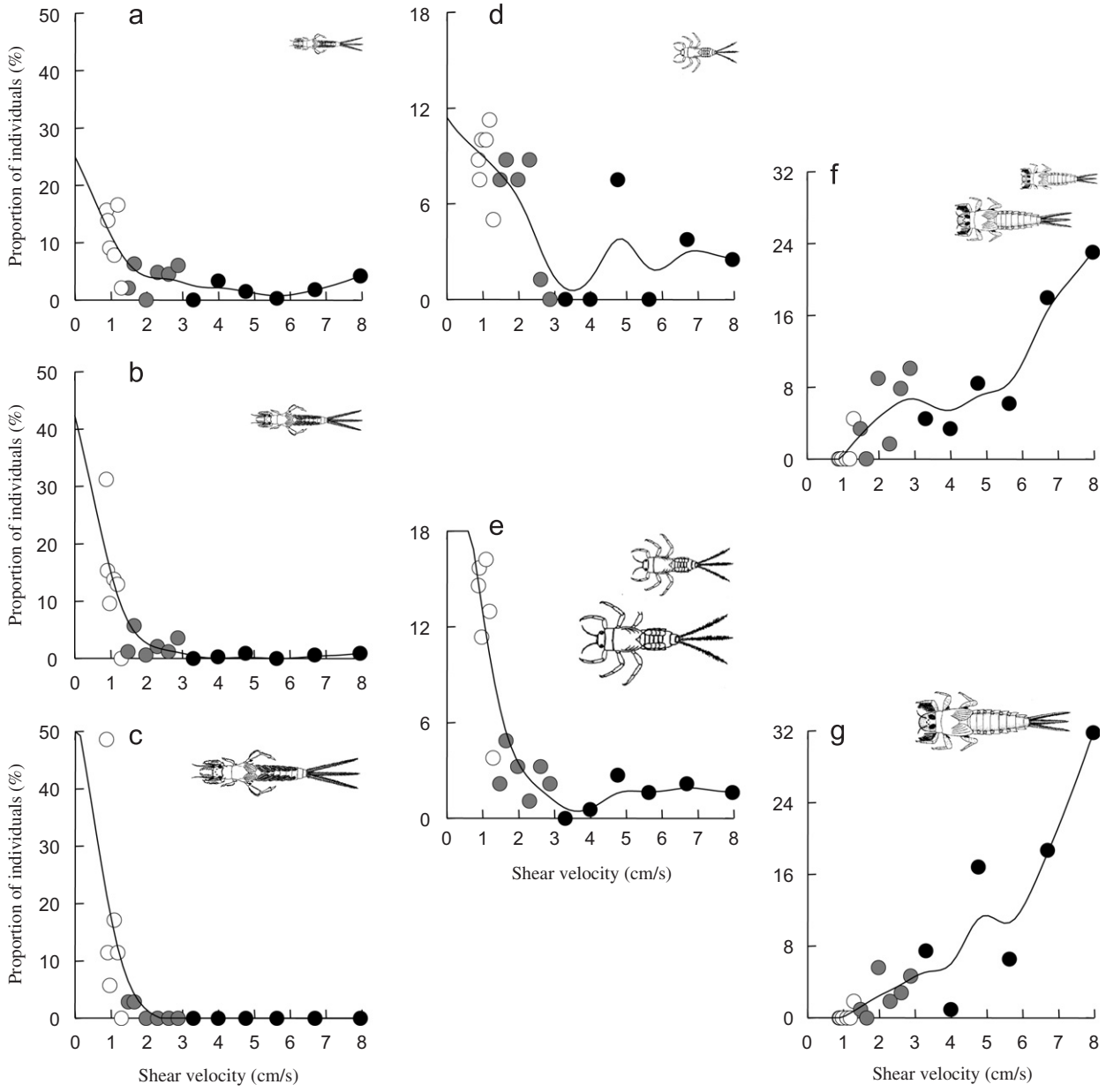

Fig. 3. Proportion of individuals (%) found in different shear velocity (cm/s) environments for different size classes of three insect species: (a) *E. virgo* size class 1, (b) *E. virgo* size class 2, (c) *E. virgo* size class 3, (d) *S. ignita* size class 1, (e) *S. ignita* size classes 2 + 3, (f) *O. rhenana* size classes 1 + 2, and (g) *O. rhenana* size class 3. For each species, size range and number of individuals used in the analyses are given in Table 1. Note that the scales of *y*-axes differ among species. White, gray, and black dots represent low (L), medium (M), and high (H) shear velocity classes, respectively (see text and Table 1). Indicative trends (curved lines) were estimated using a least squares smoothing. Insect drawings from Tachet et al. (2000).

between size classes 1 and 2 (χ^2, $p<10^{-6}$) but not significant between size classes 2 and 3 [χ^2, $p=0.13$; maybe because the number of individuals in size class 3 was low ($n=35$) with respect to the number of individuals in size class 2 ($n=333$)]. For this species, percentages of individuals in medium and high shear velocity conditions decreased between size classes 1 and 2 (χ^2, $p<0.01$ and $p<10^{-4}$, respectively), while the decrease was not significant between size classes 2 and 3 (χ^2, $p=0.24$ and 0.69, respectively). For *S. ignita*, the proportion of individuals in low shear velocity conditions increased with size (χ^2, $p<0.001$), while the proportion of individuals in medium shear velocity conditions decreased (χ^2, $p<0.01$) and the proportion of individuals in high shear velocity conditions did not change (χ^2, $p=0.29$) and remained very low.

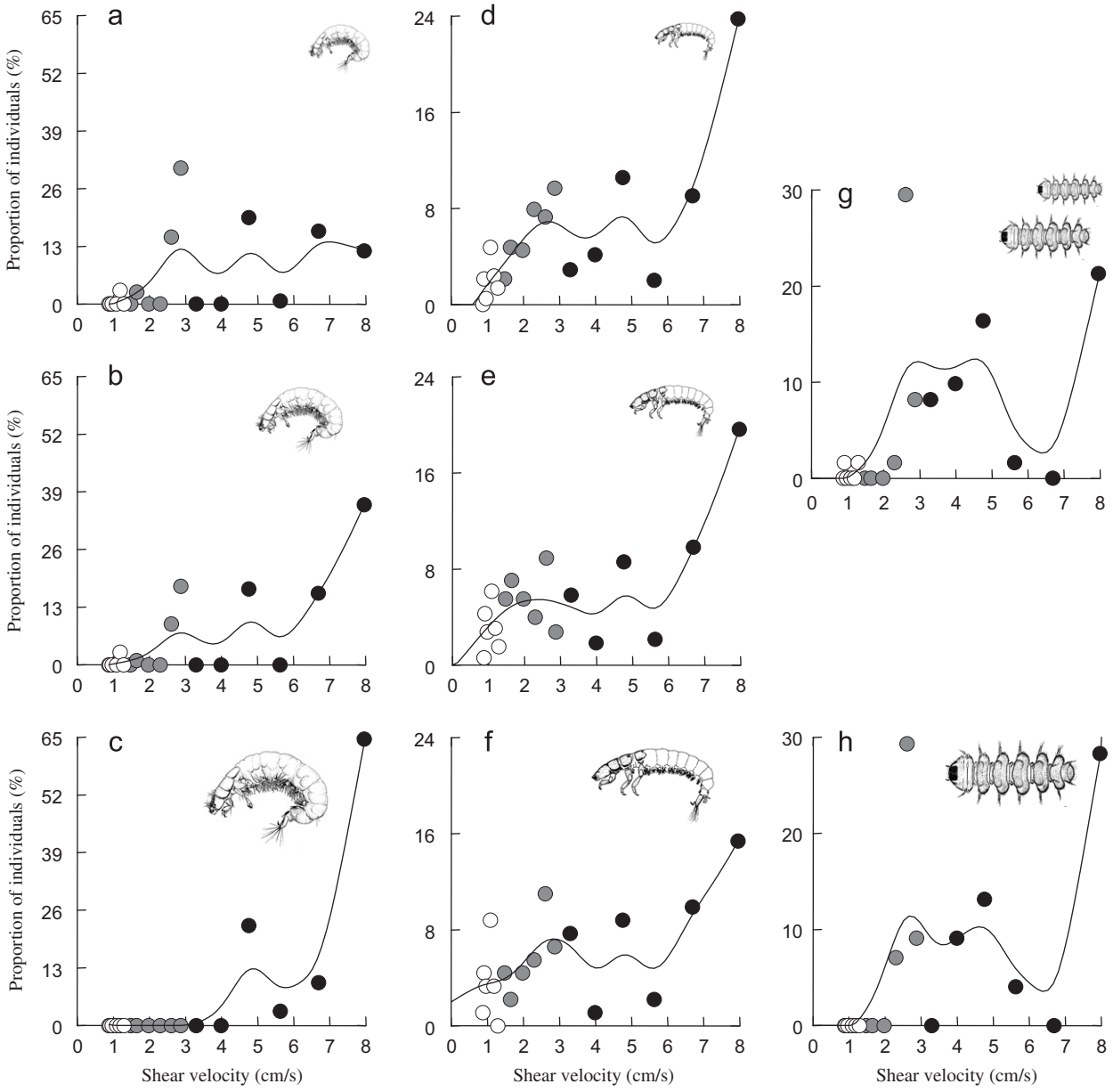

Fig. 4. Proportion of individuals (%) found in different shear velocity (cm/s) environments for different size classes of three insect species: (a) *C. lepida* size class 1, (b) *C. lepida* size class 2, (c) *C. lepida* size class 3, (d) *H. exocellata* size class 1, (e) *H. exocellata* size class 2, (f) *H. exocellata* size class 3, (g) *B. fasciata* size classes 1 + 2, and (h) *B. fasciata* size class 3. For each species, size range and number of individuals used in the analyses are given in Table 1. Note that the scales of *y*-axes differ among species. White, gray, and black dots represent low (L), medium (M), and high (H) shear velocity classes, respectively (see text and Table 1). Indicative trends (curved lines) were estimated using a least squares smoothing. Insect drawings from Moretti (1983) and Tachet et al. (2000).

Discussion

Shear velocity use of larvae

Obviously, the quantification of habitat preferences of aquatic invertebrates should ideally involve seasonally replicated samples in several streams to assess the variability due to habitat availability, biotic interactions, discharge, etc. (see examples in Dolédec et al., 2007). In the present work, we only considered one season in one Mediterranean stream to assess hydraulic habitat use of six species at a given water discharge (i.e. with a given hydraulic habitat availability). We were able to define local hydraulic preferences for these six species because a wide range of hydraulic conditions were encountered in our sampling reach. Moreover, real shifts in habitat use should be determined by following populations over time (Hanquet, Legalle, Garbage, & Céréghino, 2004). Nevertheless, such studies are very difficult to carry out

in situ. Therefore, even though we only have one season, we hypothesized that the observed differences in habitat use with invertebrate size represented successive shifts in habitat use during their growth.

E. virgo and *S. ignita* were found in low shear velocity conditions and are usually considered as limnophilic species (Tachet et al., 2000). *E. virgo* is an active filter-feeding species that constructs U-shape burrows with its sharp forelegs in fine particle substratum (i.e. low shear velocity habitats). Individuals of this species do not depend on the river current to get food as they filter water by maintaining almost continuous ventilation current through their burrow with their mobile gills (Stief, Altmann, De Beer, Bieg, & Kureck, 2004). This current also provides a high enough oxygen concentration level in the tube for this species sensitive to hypoxia (van der Geest, Soppe, Greve, Kroon, & Kraak, 2002). *S. ignita* is a scraper/grazer species feeding on live vegetation (e.g. Elliott, 1978; Willoughby & Mappin, 1988) and mainly living upon wood debris, roots, and macrophytes (Tachet et al., 2000), which are typical substrates providing hydraulic shelters in high hydraulic surrounding conditions. Therefore, the use of low shear velocity conditions by these two species corresponds to their biological traits.

C. lepida , *H. exocellata* , *O. rhenana*, and *B. fasciata* larvae were mainly found in high shear velocity conditions in our study and are considered as rheophilic species in the literature, preferring medium to high current velocity conditions (Tachet et al., 2000). However, for *C. lepida* contradicting conclusions can also be found in the literature. For instance, larvae of these species were found in areas where current speeds were reduced, near the bank or behind large boulders in the channel (Elliott, 1986). Moreover, McElhone, Davies, & Culp (1987) found that *Cheumatopsyche* sp. was more tolerant to low water velocities than *Hydropsyche* spp. in a Canadian stream whereas Dolédec and Tachet (1989) hypothesized the opposite in the Ardèche River. Such contradicting results could be explained by different habitat uses according to different species or, maybe, to different individual sizes.

Hydraulic habitat use of insect larvae may be viewed as a combined result of feeding strategies, physiological requirements but also morphological adaptations that determine their ability to maintain their position in turbulent environments or to regulate oxygen (Becker, 1987; Georgian & Thorp, 1992; Hynes, 1970; Wiley & Kohler, 1980). *C. lepida, H. exocellata*, and *O. rhenana* are passive filter feeders and require high hydraulic conditions to obtain drifting food. The two caddisflies are net-spinning species that construct fixed silken nets, perpendicular to the current, that are used to capture food (Sattler, 1958). *O. rhenana* is also a passive filtering species using its foreleg hairs as a filter (Elpers & Tomka, 1992). The two caddisfly species can temporarily resist high flow forces by attaching themselves to the substrate through their anal claws and through the production of silk yarns (Sattler, 1958; Schuhmacher, 1970). *O. rhenana* and *B. fasciata* also have morphological adaptations to high hydraulic constraints such as (i) attachment systems [a flat and concave inferior part of the labium conferring an adhesive function to the anterior part of the body and large and curved tarsal claws to cling on the substrate for *O. rhenana* (Belfiore, 1983; Studemann et al., 1992) and ventral suckers for *B. fasciata* (Frutiger, 2002)] and (ii) a dorso-ventrally flattened body (Courtney, 2000; Elliott, Humpesch, & Macan, 1988; Elpers & Tomka, 1992), which should be a morphological adaptation to live in the bottom boundary layer where flow constraints are low due to bottom proximity (Statzner & Holm, 1982; Weissenberger, Spatz, Emmans, & Schwoerbel, 1991). One can hypothesize that allometric growth could change such morphological features, modify their efficiency to resist high flow constraints and, therefore, induce successive habitat shifts during ontogeny. Allometric growth is, indeed, a common feature of larval development, ensuring most essential organs for primary functions to be first developed (Osse, van den Boogaart, van Snik, & van der Sluys, 1997).

Shear velocity use of larvae for different size classes

For *H. exocellata* and *B. fasciata*, all the sampled size classes followed the general pattern of habitat use of the whole species, and the percentages of individuals colonizing each hydraulic condition were comparable between the different size classes. In contrast, individuals of the four other species showed significant changes in their hydraulic habitat use as body size increased.

A significant proportion of individuals of *E. virgo* and *S. ignita* seemed to shift from medium to low shear velocity habitats with increasing size. Two hypotheses may explain this behavior: (1) larvae maintain the turbulence conditions around their body (i.e. their Reynolds number, examples in Peckarsky, Horn, & Statzner, 1990; Statzner & Borchardt, 1994), for a given body shape, this behavior is supposed to promote stability in at least four relevant physical factors: the diffusion of gases such as oxygen through boundary layers, abrasion by suspended solids, and the lift and drag coefficients (Statzner & Holm, 1982) and/or (2) larvae seek low velocity conditions (e.g. near the banks) for emergence (Alba-Tercedor, 1990; Hynes, 1976). Such differences in habitat use between larvae of different sizes could partly explain the seasonal variability in the hydraulic preferences of *S. ignita* observed by Dolédec et al. (2007).

In contrast, some individuals of *O. rhenana* seemed to shift from medium to high shear velocity habitats with increasing size. This behavior may reflect changes in

oxygen requirements when growing: as larger individuals develop lower surface area to volume ratio (Kovalak, 1978), they may search for more oxygenated (i.e. more turbulent) habitats. Moreover, Buffagni et al. (1995) suggested that "older larvae are able to maintain better their position in the current". Therefore, morphological adaptations to high shear velocity conditions (such as a flattened body, the presence of an adhesive labium, claws) may increase in efficiency with increasing size, enabling larger stages of *O. rhenana* to colonize high shear velocity habitats in which they would escape from predators. Predators are usually larger than their prey and therefore have to suffer higher flow constraints than prey in terms of Reynolds number (Statzner & Borchardt, 1994). The same trend was observed for individuals of *C. lepida,* with the largest individuals being more numerous in habitats with high shear velocity conditions. As hypothesized by Collier et al. (1995) for Hydrobiosidae (Insecta: Trichoptera) species, morphological adaptation to high shear velocity conditions, such as anal claws, may be more effective for larger individuals of *C. lepida*. Moreover, pupal mortality of trichopteran species is known to be partly due to siltation (Rutherford & Mackay, 1986), and largest larvae of *C. lepida* may progressively colonize habitats with high hydraulic constraints to reduce the risk of siltation during the motionless pupal stage. Nevertheless, we must consider that we did not sample all of the size classes of this species. Indeed, last larval instars (larger than the largest individuals of the present study) have been later observed near the river banks (i.e. in low hydraulic habitat conditions, unpublished data) probably because of emergence needs.

These results confirmed for the studied species that, as demonstrated for fish, aquatic insect larvae can display different hydraulic habitat use while growing. Depending on the species, individuals may shift to lower or higher shear velocity conditions and changes in morphology (e.g. potential adaptations to high hydraulic velocity conditions) and/or in behavior most likely determine these habitat shifts. However, more knowledge is needed on these points to better understand the dynamics of benthic invertebrate habitat use in rivers. As for fish, the hydraulic preferences of the different size classes of benthic invertebrate species should be considered in instream habitat models. Otherwise, determining optimal flow criteria at the species level (i.e. mixing all stages) may result in the loss of habitat for a key developmental stage and, subsequently, to bottlenecks in population dynamics.

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